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RESEARCH PAPER

Effects of *Lactobacillus* fermentation on the phenolic and flavor substances of coconut water

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Abstract

In this study, *Lactobacillus* strains with beneficial biofunctions were screened and applied to ferment coconut water. The effects of *Lactobacillus* fermentation on the phenolic and flavor components of coconut water were investigated. The results showed that the strains *Lactobacillus casei* U2.1 and *Lactobacillus paracasei* M1.5 possessed excellent DPPH radical scavenging (30.91%) and α-amylase inhibitory activity (57.44%), and both of them survived over 50% in simulated gastrointestinal fluids. The co-fermentation of the two strains elevated the total phenolic content of coconut water by 19%, with a significant increase in free phenols and insoluble glycoside-type phenols ($P < 0.05$), indicating that lactobacilli fermentation promoted the release and conversion of phenolics. Through gas chromatography-mass spectrometry (GC-MS) analysis, it was found that the variety of volatile flavor substances increased by 27 species after fermentation, and the generation of key flavor substances (phenylethanol and ethyl caprylate) enhanced the aroma quality of the coconut water. In addition, the accumulation of potential physiologically active components (palmitoleic acid and cis-5-dodecenoic acid) further enhanced the nutritional value of the product. In conclusion, the co-fermentation of the two strains improved the nutritional value and flavor of coconut water, which provided a theoretical basis for the development of fermented coconut water beverage.

Keywords

Coconut, *Lactobacillus*, phenolic, volatile flavor substances

Introduction

Coconut (*Cocos nucifera* L.) belongs to the Arecaceae family, and is an important cash crop, mainly distributed in Indonesia, Brazil, the Philippines and other regions. In mature coconuts, coconut water accounts for about 18% of the total weight. Coconut water is a clear nutritious liquid from the endosperm of the coconut, with a unique coconut flavor, rich in minerals, vitamins and electrolytes, making it a natural electrolyte drink. Meanwhile, coconut water is rich in phenols and flavonoids, which makes it a high-quality fermentation raw material. Coconut water has antioxidant, hypolipidemic antibacterial and antidiabetic properties (DebMandal et al. 2011). Coconut water can be categorized into immature and mature coconut water based on its maturity at the time of harvest. Raw coconut water is low in fat, contains sugar, amino acids, vitamins and minerals and can be consumed directly or processed into various beverages (Hahn 2012). The nutritional value of mature coconut water does not change significantly, but the increase in crude fat content leads to deterioration in flavor (Zhang et al. 2018a, 2018b). Moreover, coconut water is often discarded during the production of coconut milk or cream, resulting in a waste of resources. Therefore, new processing methods need to be explored to develop high-value coconut water products.

Fermentation is a traditional method of food processing and preservation, and *Lactobacillus*- fermented products representing a significant category. Lactobacilli are a group of active microorganisms that improve the host's intestinal

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environment and have positive effects on health, such as promoting nutrient absorption, alleviating lactose intolerance, and regulating intestinal health (Teng et al. 2020). Microorganisms of the genus *Lactobacillus* are mainly associated with the production of fermented foods (Plessas et al. 2017), altering the biochemical and organoleptic properties of fermented raw materials and providing abundant nutrients such as minerals, vitamins, amino acids and digestive enzymes (Ray et al. 2016; Du et al. 2024; Yang et al. 2024). In addition, lactobacilli are widely used as probiotics due to their high safety and diverse probiotic functions.

Lactobacillus fermentation can change the composition of the substances in the plant-based substrate, so that the flavor substances in the product can be changed and the functionality can be enhanced. It has been shown that the fermentation of *L. plantarum* increased the total phenolics and antioxidant capacity in blueberry juice (Zhang et al. 2021). Furthermore, Kantachote (2017) and Giri (2018) found that coconut water fermented by different *Lactobacillus* had improved flavor and nutrients in the product as well as a better storage quality.

In this study, *Lactobacillus* with good basic properties and potential physiological functions (antioxidant and hypoglycemic) were screened and applied to coconut water fermentation. And the effects of *Lactobacillus* fermentation on the content, composition and type of phenolics and volatile flavor substances in coconut water were further investigated. The result would provide a theoretical basis for the development of novel fermented coconut water products.

Materials and methods

Experimental reagents

Coconut water: The coconuts produced in Wenchang, Hainan, were cracked open to extract the water, which was then filtered through four layers of gauze, mixed, and stored at 4 °C.

Strain source: *L. casei* U2.1, *L. paracasei* O3.3, *L. fermentum* S1.5, *L. paracasei* M1.5 were isolated from traditional fermented foods (Chinese sauerkraut, kimchi) and preserved in College of Food Science and Technology, Henan Agricultural University, and *L. rhamnosus* LGG was isolated from live bacterial powder.

All other reagents used in the test were analytically pure and purchased from general suppliers.

Strain culture conditions

The strains were streaked onto MRS solid medium using the streak plate method and subsequently incubated at 37 °C for a duration of 48 h. Subsequent to this period, a well-isolated single colony was transferred to MRS liquid medium and cultivated at the same temperature for an additional 24 h. The strains were subcultured twice in this manner.

Preparation of Bacterial Suspension: After activating *Lactobacillus* for two generations, the bacterial cells were separated by centrifugation (10000 × g, 4 °C, 5 min). The concentration of viable bacteria was subsequently adjusted to 1×10^8 CFU/mL using phosphate-buffered saline (PBS, pH 7.0) based on the viable count.

Basic properties of *Lactobacillus* strains

Growth curves, pH and acidity measurement

The activated bacterial solution was transferred to MRS liquid medium at an inoculum of 1% (v/v) and incubated at 37 °C for 24 h. Samples were taken at 0 h, 2 h, 4 h, 8 h, 12 h, 14 h, 16 h, 18 h, 20 h, 22 h, and 24 h to determine the OD_{600}, pH values, and acidity. A pH meter was used to measure the pH, while the total acidity, expressed as lactic acid, was determined by the titration method.

Simulated gastrointestinal fluid tolerance assay

Preparation of simulated gastric and intestinal fluids was performed with reference to Son et al. (2018).1 mL of bacterial suspension was inoculated into 9 mL of simulated gastric and simulated intestinal fluids, respectively, and incubated with shaking and mixing at 37 °C for 3 h. Samples were taken at 0 and 3 h to calculate the number of viable bacteria in the sample by the plate count method. The results were calculated according to formulas (1) and (2).

$$N_{\text{Gas.}}(\%) = \frac{\text{Num}_{3\text{h}}}{\text{Num}_{0\text{h}}} \times 100\% \quad (1)$$

Where $N_{Gas.}$ indicates gastric fluid tolerance survival rate.

$$N_{\text{Int.}}(\%) = \frac{\text{Num}_{3\text{h}}}{\text{Num}_{0\text{h}}} \times 100\% \quad (2)$$

where $N_{Int.}$ indicates intestinal fluid tolerance survival rate.

Measurement of the reducing power of the strains

1 mL of the bacterial suspension was mixed with 2.5 mL $K_3[Fe(CN)_6]$ (1%) solution and 2.5 mL of PBS buffer (0.2 mol/L, pH 6.6). After a water bath at 50 °C, the suspension was cooled in ice water for 5 min. Subsequently, 2.5 mL trichloroacetic acid (TCA) solution (10%) was added to the cooled sample, followed by centrifugation at 4 °C and 3500 × g for 10 minutes. Following centrifugation, 2.5 mL of the supernatant was extracted, to which 2.5 mL of distilled water and 0.5 mL $FeCl_3$ (0.1%) solution were added. The absorbance was then measured at 700 nm (Li et al. 2012).

Measurement of free radical scavenging rate of ATBS

The ABTS radical-scavenging activity was determined spectrophotometrically using the method described by Delgado et al. (2019). The ABTS working solution was prepared by diluting ABTS stock (7.68 g/L ABTS, 13.24 g/L $K_2S_2O_8$ in pure water) with anhydrous ethanol to achieve a specific absorbance value of 0.7 ± 0.02 (A value). A sample of bacterial suspension (1.0 mL) was mixed with the

ABTS working solution (5 mL) and incubated in the dark at room temperature for 5 minutes before the absorbance was measured. The absorbance of the sample was measured at 734 nm as A_0. The results were calculated using formula (3).

$$N_{ABTS.}(\%) = \frac{A_0 - A}{A} \times 100\% \quad (3)$$

Where $N_{ABTS.}$ indicates the ABTS free radical scavenging rate.

Measurement of DPPH scavenging capacity

The scavenging capacity of DPPH free radicals was determined spectrophotometrically (Oh et al. 2020). Briefly, 2.0 mL of bacterial suspension was mixed with 4.0 mL of DPPH solution (0.1 mmol/L). After incubation for 25 min at room temperature in the dark, the reaction mixture was centrifuged at 5000 × g for 5 min at 4 °C. Sample controls were prepared by mixing with an equal volume of anhydrous ethanol instead of the DPPH solution. For the control group, distilled water was used in place of the DPPH solution. The results were calculated using formula (4).

$$N_{DPPH.}(\%) = \left(1 - \frac{OD_S - OD_{SC}}{OD_C}\right) \times 100\% \quad (4)$$

Where $N_{DPPH.}$ denotes DPPH clearance rate. OD_S is sample group; OD_{SC} is the sample control group; and OD_C is the control group.

Measurement of α-glucosidase inhibition rate

α-glucosidase inhibition rate was performed according to Zhang et al. (2007). 100 μL of α-glucosidase (0.4 U/mL) was added to 50 μL of bacterial suspension and incubated for 10 minutes at 37 °C. Subsequently, 100 μL of PNPG (2.5 mmol/L) was added to each reaction tube, and incubation continued for 30 minutes at 37 °C. Finally, the reaction was terminated by the addition of 50 μL of Na_2CO_3 solution (1 mol/L).The absorbance at 405 nm was measured for the sample group, sample control group, control group and blank group. The results were calculated according to formula (5).

$$N_{Glu.}(\%) = \left(1 - \frac{OD_S - OD_{SC}}{OD_C - OD_R}\right) \times 100\% \quad (5)$$

In this case, the sample control is a mixture of PNPG and sample without added enzyme. The control is a mixture of PNPG and enzyme without added sample. The blank group was PBS solution (0.1 mol/L, pH 6.8). Where $N_{Glu.}$ denotes the rate of glucosidase inhibition. OD_S is the sample group; OD_{SC} is the sample control group; OD_C is the control group; OD_B is the blank group.

Measurement of α-amylase inhibition rate

α-amylase inhibition was performed according to Meng et al. (2016). 0.25 mL of bacterial suspension was mixed with 0.25 mL of α-amylase (1.0 mg/mL) and incubated for 10 min at 37 °C. Subsequently, 0.5 mL of starch solution (1%) was added, and the incubation was continued for another 5 min at 37 °C. The reaction was terminated by adding 1 mL of DNS solution, and the mixture was then heated in a boiling water bath for 5 min before being rapidly cooled to room temperature. The reaction products were diluted using PBS. The absorbance at 540 nm was measured for the sample group, sample control group, control group and blank group. The results were calculated using formula (6).

$$N_{Amy.}(\%) = \left(1 - \frac{OD_S - OD_{SC}}{OD_C - OD_B}\right) \times 100\% \quad (6)$$

In this case, the sample control is a mixture of starch solution and sample without added enzyme. The control is a mixture of starch solution and enzyme without added sample. The blank group was PBS solution (0.1 mol/L, pH 6.8). Where $N_{Amy.}$ denotes amylase inhibition rate. OD_S is the sample group; OD_{SC} is the sample control group; OD_C is the control group; OD_B is the blank group.

Coconut water fermentation

Preparation of fermented coconut water

For fermentation, a mixture of *L. paracasei* M1.5 and *L. casei* U2.1, obtained from previous screening, was used as the fermenting agent at a mixing ratio of 1:1 (n:n). And the inoculum inoculated into the fermentation material was 4% (v/v) of the inoculum to the fermentation material. Following inoculation, the coconut water was fermented at a constant temperature of 35 °C for 22 h. At the conclusion of the fermentation process, the products were placed in a cold room at 4 °C for 24 h of post-ripening.

Determination of phenolic content

Polyphenol standard curve

Standard curves for phenol were created using the Folin-Ciocalteu reagent (Managa et al. 2021). Standard solutions of varying concentrations were treated with the Folin-Ciocalteu reagent (10%, 2.5 mL) for 8 min, followed by the addition of sodium carbonate (7.5%, 2 mL). After incubation in the dark for 60 min, the absorbance was measured at 765 nm. The standard curve was then plotted with gallic acid concentration on the horizontal axis and absorbance values on the vertical axis.

Preparation of free phenolics

The extraction of phenol followed the method described by Ayaz et al. (2005) with slight modifications. 5 mL of fermented coconut water was taken and extracted with 25 mL of 80% (v/v) methanol solution. Subsequently, the mixture was centrifuged (10000 × g, 10 min, 4 °C). The filtrate was extracted twice by repeating the same procedure and the resulting supernatant was collected as soluble phenolic components. The soluble phenol obtained through centrifugation was concentrated to dryness using a rotary evaporator at 35 °C. Subsequently, the concentrate

was redissolved in 40 mL of distilled water. The mixture was then degreased using hexane, and the aqueous phase was separated. The aqueous phase was separated three times using ethyl acetate. The liquid from the combined extractions was concentrated under vacuum. The extract was redissolved in 10 mL of 80% (v/v) methanol to obtain the free phenol fraction.

Preparation of soluble ester phenolics

The aqueous phase from the separation in 2.4.2.2 was hydrolyzed by adding 40 mL of NaOH (2 mol/L) for 4 h (37 °C, 150 rpm) and then acidified with HCl (6 mol/L) to pH 2.0. The mixture was degreased, extracted, dried, and reconstituted according to section "Preparation of free phenolics". The result of the re-solubilization was the soluble ester phenol fraction.

Preparation of soluble glycoside phenolics

The soluble glycosidic phenol fraction was extracted from the water phase following the ethyl acetate extraction of the soluble ester phenolic fraction obtained in section 2.4.2.3. The water phase was hydrolyzed using 10 mL of 6 mol/L HCl in a water bath at 85 °C for 30 min and then adjusted to pH 2.0 with 10 mol/L NaOH. The mixture was then defatted, extracted, dried, and reconstituted according to the protocol outlined in section "Preparation of free phenolics".

Preparation of insoluble ester phenolics

The residue obtained in section 2.4.2.2 was initially subjected to digestion with 40 mL of 2 mol/L NaOH while being agitated (37 °C, 150 rpm) for 4 hours. The supernatant of the mixture, after centrifugation (11,960 × g, 10 min, 4 °C), was acidified to pH 2.0 with 6 mol/L HCl. The mixture was then defatted, extracted, dried, and redissolved following the procedures outlined in section "Preparation of free phenolics".

Preparation of insoluble glycoside phenolics

The insoluble glycosidic phenol fraction was extracted from the residue obtained in section 2.4.2.5 (after centrifugation). The residue was hydrolyzed with 25 mL of 2 mol/L HCl in a water bath (at 85 °C for 60 minutes). The supernatant of the mixture, following centrifugation (at 11,960 × g for 10 minutes at 4 °C), was adjusted to pH 2.0 using 10 mol/L NaOH. Subsequently, the mixture underwent defatting, extraction, drying, and was redissolved as per section "Preparation of free phenolics".

Determination of phenolic content in different forms

The method of Gong et al. (2017) was referred to with slight modification. The extracts (prepared in sections 2.4.2.2–2.4.2.6) were treated with a 10% (v/v) Folin-Ciocalteu reagent (2.5 mL) at 25 °C for 8 minutes. Subsequently, 7.5% (w/v) Na_2CO_3 (2 mL) was added to the mixture. The reaction was carried out in the dark for 60 minutes, and the absorbance of the mixture at 765 nm was measured. A standard curve was generated using gallic acid, and the results were expressed as Gallic acid equivalent (GAE) mg/g dry weight (DW).

Determination of monomer phenolics content

The determination was carried out using a 1260 Infinity II liquid chromatograph (Agilent, USA). The separation was performed on a Supersil ODS2-C18 column (4.6 mm × 250 mm, 5 μm). The column temperature was maintained at 35 °C. The mobile phase consisted of two solvents: (A) 1% formic acid and (B) methanol. Gradient elution was achieved by adjusting the volume ratio of solvent B in the mobile phase at a flow rate of 1 mL/min. The injection volume was 20 μL. All samples were analyzed using the diode array detector (DAD) at 280 nm. Components in phenol extracts were tentatively identified by comparing their retention time and peak area to those of standards under identical analysis conditions.

Determination of volatile flavor substances

A 7890A/5975C gas chromatography-mass spectrometer (Agilent, USA) was utilized for the analysis. A 10 mL sample was placed in a 15 mL vial, heated, and equilibrated to 80 °C for 30 minutes. Subsequently, the solid phase microextraction (SPME) probe was inserted into the vial and adsorbed in the headspace for 20 min with magnetic stirring at a speed of 100 × g.

Separation was conducted on a capillary column DB-WAX (30 mm × 0.25 mm, 0.25 μm). The inlet port temperature was set at 250 °C, and the SPME was inserted into the inlet well for desorption for 5 minutes. The temperature was programmed to increase: starting at 35 °C, held for 2 minutes, then ramped up to 230 °C at a rate of 5 °C/min, and held for 8 minutes. The carrier gas (He) flow rate was maintained at 1.0 mL/min without a shunt.

Mass spectrometry conditions: ion source temperature set at 230 °C, quadrupole temperature at 150 °C, electron energy at 70 eV, and the mass scan range was 33–450 amu.

Statistical analysis

All data were expressed as mean ± standard deviation calculated from the results of 3 or more experiments. Data were analyzed and plotted using SPSS 26 (SPSS, Inc., Chicago, IL, USA) and ORIGIN 2021(Origin Lab Co., Northampton, MA, USA). Results were considered significant at $P < 0.05$ using one-way ANOVA.

Results and discussion

Basic properties of the strains

Lactobacillus can utilize the monosaccharides present in coconut water to produce organic acids, and its growth and acid production capabilities significantly influence the fermentation process of coconut water. Consequently,

changes in pH and growth capacity can serve as reliable indicators to evaluate the suitability of *Lactobacillus* as a fermenting strain (Salmerón et al. 2015). The growth curves of *Lactobacillus*, along with the changes in pH and acidity, are illustrated in Fig. 1A–C. The lag phase for *Lactobacillus* incubated at 37 °C was observed to be 2 h. During the initial 18 h, no significant differences were noted in the growth rates and acid-producing capacities among *L. paracasei* M1.5, *L. casei* U2.1 and *L. paracasei* O3.3. However, the growth rate and acid-producing capacity of *L. fermentum* S1.5 were significantly lower than those of the other three *Lactobacillus* strains. *L. casei* U2.1 and *L. fermentum* S1.5 entered the stabilization phase at 18 hours, while *L. paracasei* M1.5 and *L. paracasei* O3.3 exhibited prolonged growth periods, entering the stabilization phase at 22 h. The pH of the culture broth began to stabilize after 14 h, with *L. fermentum* S1.5 displaying a significantly higher pH compared to the other three lactic acid bacteria strains.

The results of the survival rate of lactic acid bacteria after incubation in simulated gastric and intestinal fluids are presented in Fig. 1D. The study by Megur et al. (2023) showed that excellent tolerance could be indicated when the number of surviving microorganisms was greater than 1×10^7 cfu/mL. Analysis of the survival rate data revealed that *L. paracasei* M1.5 demonstrated exceptional gastrointestinal tolerance. The viable counts of *L. paracasei* M1.5, *L. casei* U2.1, and *L. fermentum* S1.5 exceeded 1×10^7 cfu/mL, indicating good tolerance. In summary, *L. paracasei* M1.5, *L. casei* U2.1, and *L. fermentum* S1.5 were classified as lactobacilli with gastrointestinal tolerance.

In conclusion, *L. paracasei* M1.5 and *L. casei* U2.1 exhibited robust growth and acid production capabilities, significantly altering the acidity of the culture broth, making them suitable for use as fermenters in coconut water fermentation.

Antioxidant capacity of strains

The antioxidant function of food products is of increasing interest due to its potential positive impact on human health. The antioxidant function is mainly due to the bioactive substances they contain (Abountiolas et al. 2018). In this study, three indices such as total reducing power, DPPH and ABTS radical scavenging capacity were selected to evaluate the antioxidant capacity of lactic acid bacteria. The results, as shown in Fig. 2, showed that the DPPH radical scavenging rates of the four *Lactobacillus* strains were *L. casei* U2.1 (30.91% ± 0.012) > *L. paracasei* O3.3 (12.40% ± 0.009) > *L. fermentum* S1.5 (7.45% ± 0.006) > *L. paracasei* M1.5 (6.33%±0.008). The ABTS free radical scavenging activity of the four *Lactobacillus* strains was *L. paracasei* O3.3 (41.82% ± 0.012) > *L. casei* U2.1 (41.72% ± 0.017) > *L. paracasei* M1.5 (33.83% ± 0.007) > *L. fermentum* S1.5 (22.24% ± 0.008).The total reducing power of *L. fermentum* S1.5 and *L. casei* U2.1 was better.

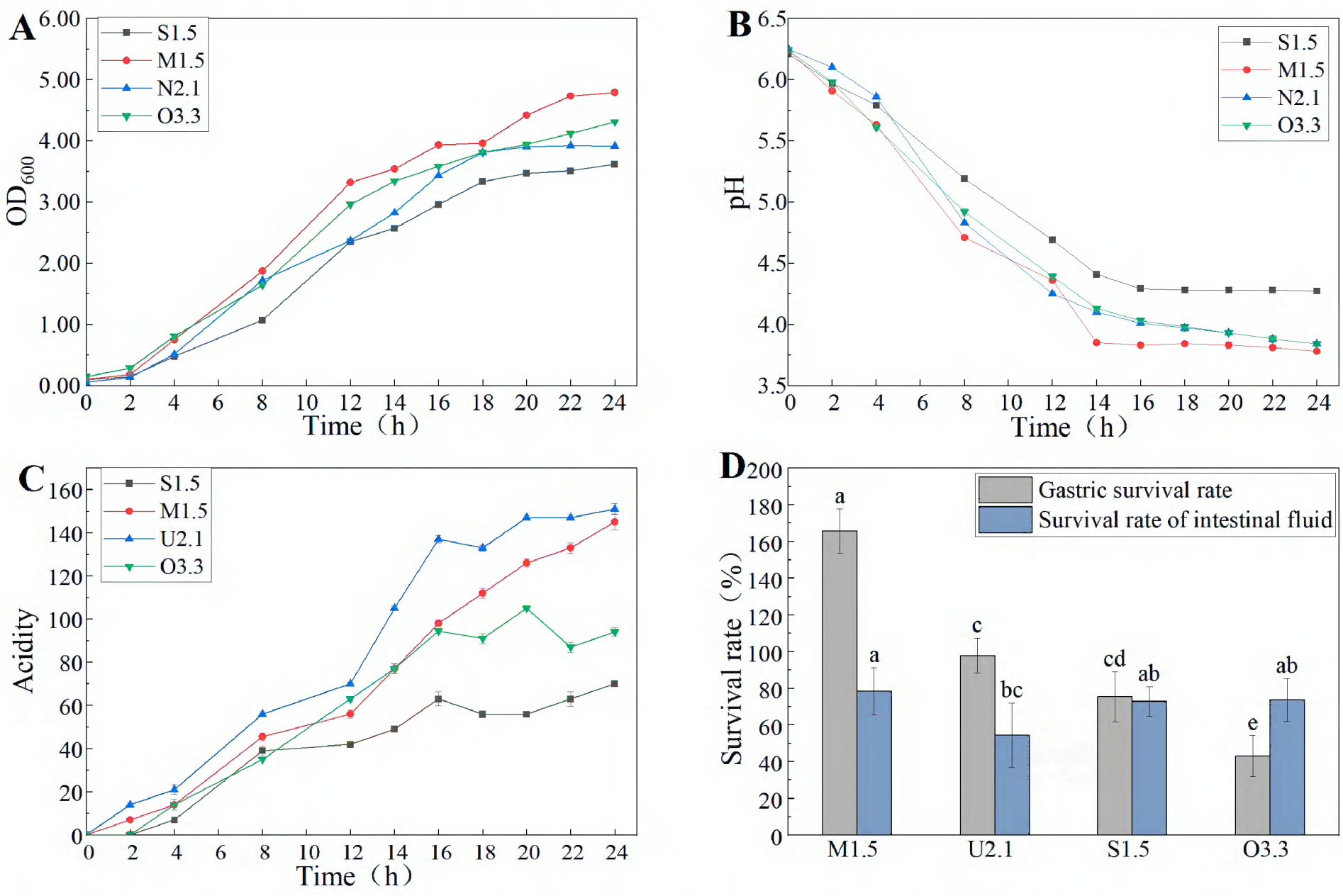

Figure 1. Basic properties of *Lactobacillus*. **A.** Growth curve; **B.** PH change curve; **C.** Acidity change curve; **D.** Gastrointestinal tolerance survival.

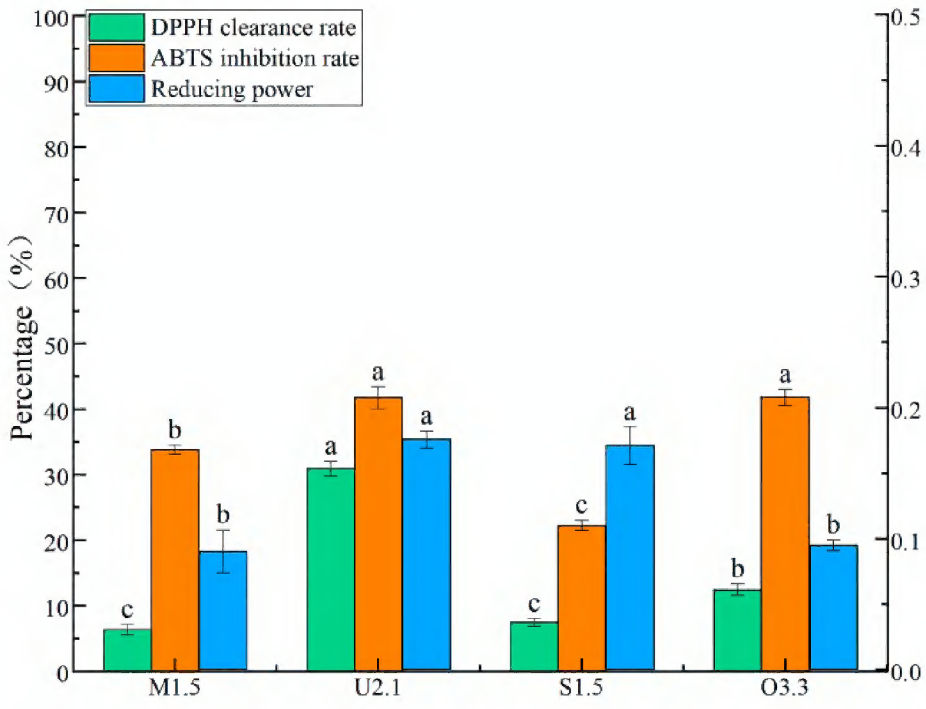

Figure 2. Antioxidant capacity of *Lactobacillus*.

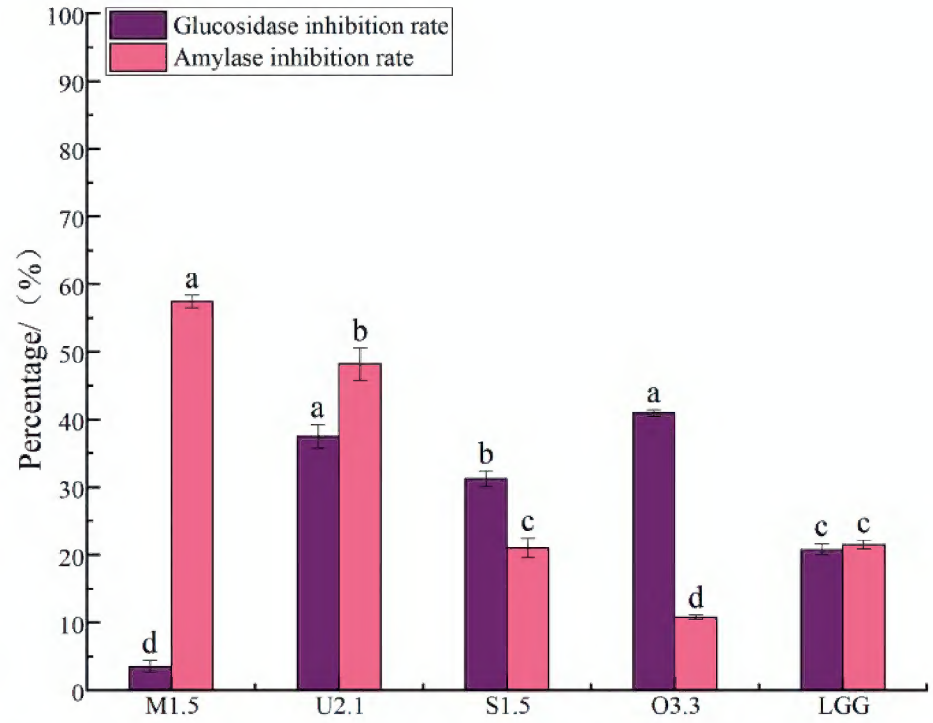

Figure 3. Hypoglycemic capacity of *Lactobacillus*.

Xu et al. (2011) showed that the ability of *Lactobacilli* to scavenge DPPH radicals was positively correlated with the concentration of extracellular polysaccharides they produced and the activity of the extracellular polysaccharides. The scavenging of DPPH radicals is a process whereby the radical binds to a hydrogen atom, and DPPH forms stable compounds after acquiring hydrogen atoms (Berset et al. 1995; Berset et al. 1997; Tsimogiannis et al. 2006). *L. casei* U2.1 may produce more extracellular polysaccharides capable of providing hydrogen atoms to DPPH or other substances that achieve antioxidant activity by providing hydrogen atoms during growth. Unlike DPPH, scavenging of ABTS radicals is considered to be an electron-transfer reaction that achieves free radical scavenging mainly by obtaining electrons through a reaction with antioxidant substances (Vassalle et al. 2004). *L. paracasei* O3.3 had the strongest scavenging capacity of ABTS radicals. In scavenging both DPPH and ABTS radicals, *L. casei* U2.1 showed good scavenging ability.

The scavenging capacity of two free radicals, ABTS and DPPH, was positively correlated with the strength of total reducing power, with some exceptions. Differences in the metabolism of lactic acid bacteria lead to differences in antioxidant capacity. *L. fermentum* S1.5 showed poorer scavenging capacity for two free radicals, DPPH and ABTS, but higher reducing power. *L. casei* U2.1 showed good positive correlation between the two and higher total reducing power. In conclusion, *L. casei* U2.1 was the superior strain for antioxidant function.

In vitro assessment of the hypoglycemic capacity of the strains

α-Glucosidase and α-amylase are important enzymes in the process of glucose metabolism, which can hydrolyze glycosidic bonds to produce glucose, and have an important effect on human blood glucose concentration. Therefore, the inhibition rate of α-glucosidase and α-amylase was chosen as an index to evaluate the hypoglycemic function of the strain in this study. The inhibition rates of α-glucosidase and α-amylase activity by lactic acid bacteria. The inhibition rate of α-glucosidase by five strains ranged from 3.52% to 40.94%, with the positive control strain *L. rhamnosus* LGG having an inhibition rate of 29.57. And the inhibition rates of *L. casei* U2.1 (37.5% ± 1.72) and *L. paracasei* O3.3 (40.94% ± 0.46) were significantly higher inhibition than *L. rhamnosus* LGG.

The inhibition of α-amylase by lactic acid bacteria ranged from 10.77% to 57.44%. The inhibition rates of *L. rhamnosus* LGG was 21.53%, which was lower than that of *L. paracasei* M1.5 (57.44% ± 0.931) and *L. casei* U2.1 (48.21% ± 2.373). The hydrolysis of polysaccharides can be reduced by inhibiting the activities of α-glucosidase and α-amylase, which indirectly regulates the blood glucose level (Khan et al. 2023). Therefore, the inhibitory capacity of α-glucosidase and α-amylase can represent the hypoglycemic activity. *L. casei* U2.1 showed good inhibition of both indicator enzymes, suggesting the potential hypoglycemic capacity of *L. casei* U2.1.

The inhibitory effects of *Lactobacillus* strains on α-glucosidase and α-amylase could be attributed to several mechanisms. Firstly, lactic acid bacteria are known to produce various metabolites during fermentation, including organic acids (e.g., lactic acid and acetic acid), exopolysaccharides, and bioactive peptides, which may interact with these enzymes and alter their catalytic activities (Wang et al. 2014; Zhang et al. 2021). Organic acids can lower the local pH or directly bind to the active sites of the enzymes, thereby reducing their efficiency. Secondly, certain components of the bacterial cell wall or extracellular polymeric substances might adsorb or complex with the enzymes, leading to steric hindrance or conformational changes that impede substrate access. Furthermore, the production of specific inhibitory compounds through microbial metabolism, or the ability of probiotics to modulate the gut microbiota, may indirectly influence host.

Effect of *Lactobacillus* fermentation on the content and composition of polyphenolic substances in coconut water

L. paracasei M1.5 and *L. casei* U2.1 were selected as the coconut water fermentation agent based on the results of the above basic performance experiments. After 24 h of fermentation with M1.5-U2.1, the total phenol content of coconut

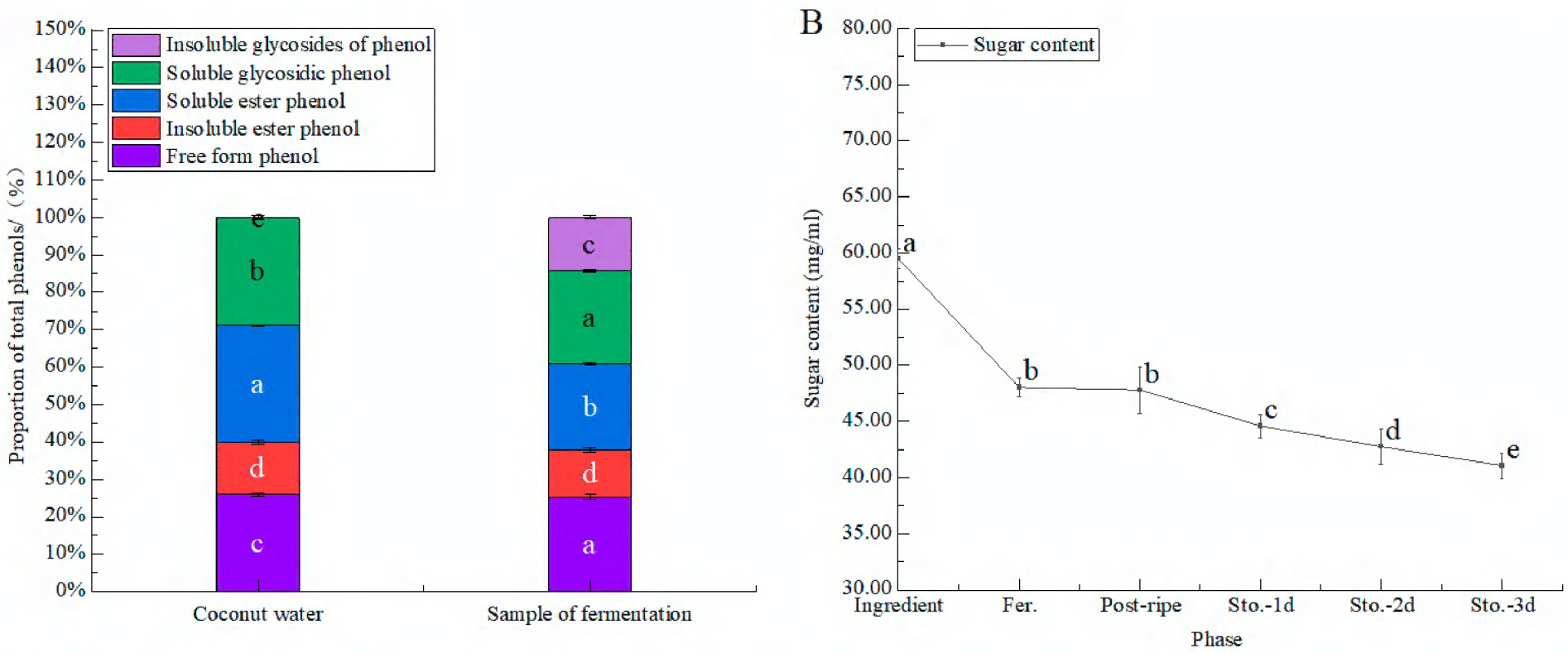

Figure 4. Effect of fermentation on phenolics in coconut water.

water was increased by 19%, and the fermentation products contained significantly more soluble glycoside phenols, insoluble glycoside phenols, insoluble lipophilic phenols, and free phenols, and a significant decrease in fat-soluble phenols (Table 1, Fig. 4). In previous studies, Ghosh et al. (2015) and Freire et al. (2017) found that fermentation of cereal slurry by *Lactobacillus* led to a significant increase in phenolic content. The increase in free phenols may be attributed to several factors: (1) the production of reducing substances through *Lactobacillus* metabolism that protect free phenols from oxidation; (2) the generation of new free phenolics via glycosylation and methylation during metabolic processes; and (3) the enzymatic catabolism of macromolecules by *Lactobacillus* during fermentation (Jamal et al. 2011; Hur et al. 2014). Phenolics have a variety of functional properties and the increase in phenolic content in fermented coconut juice may indicate elevated levels of phenols with antioxidant and hypoglycemic functions.

Coconut water contains phenolics such as epicatechin, p-hydroxybenzoic acid, butyric acid, o-coumaric acid, p-coumaric acid and caffeic acid (Mahayothee et al. 2016). Among them, epicatechin, p-hydroxybenzoic acid, butyric acid, and p-coumaric acid have been shown to be phenolics with hypoglycemic activity and antioxidant activity (Hii et al. 1985; Best et al. 2007; Youl et al. 2010; Kilic et al. 2013), and the fermentation of *Lactobacillus* may cause changes in their contents. Therefore, in this study, we chose to analyze the content of the above-mentioned monomer phenols in coconut water.

The experimental results are shown in Table 2. Fermentation increased p-hydroxybenzoic acid by 75%, with no significant change in syringic acid content, while caused decrease in epicatechin, p-coumaric acid and caffeic acid content by 14%, 16.5% and 34%, respectively. The depletion of antioxidant phenols such as epicatechin, caffeic acid and p-coumaric acid may be related to the protective effect of antioxidants. Clark et al. (2008) reported that antioxidants in fermented wine produced a depletion of the protective effect on other oxidation-prone substances. Additionally, the content of p-coumaric acid was influenced by the hydrolysis of p-coumaroylated anthocyanins. Flavanol-type phenolic compounds such as epicatechin underwent polymerization and subsequent oxidation (Clark et al. 2010), all of which led to a decrease in monomeric phenol content. The increase in p-hydroxybenzoic acid content may be related to the action of aldehyde dehydrogenase (Payet et al. 2016), which converted p-hydroxybenzaldehyde analogs to p-hydroxybenzoic acid. In addition, p-hydroxybenzoic acid can be biosynthesized *via* the mangiferolic acid pathway. In this pathway, phosphoenolpyruvic acid produced by glycolysis was converted to chorismic acid and further produces p-hydroxybenzoic acid (Mir et al. 2015; Li et al. 2020).

Table 1. Effect of fermentation on phenolic contents.

Sample	Polyphenol content (μg/mL)					
	Free phenol	Insoluble ester phenol	Soluble ester phenol	Soluble glycosidic phenol	Insoluble glycosidic phenol	Total phenol
Coconut water	17.62 ± 0.26^{Bc}	9.56 ± 0.45^{Bd}	21.13 ± 0.09^{Aa}	19.60 ± 0.43^{Bb}	ND	67.91 ± 0.25^{B}
Fermentation broth	20.44 ± 0.51^{Aa}	10.21 ± 0.40^{Ad}	18.56 ± 0.31^{Bb}	20.19 ± 0.23^{Aa}	11.49 ± 0.37^{Ac}	80.89 ± 0.46^{A}

Table 2. Effect of fermentation on the content of monomeric phenols.

Sample	Monomer phenol content (μg/mL)				
	Epicatechin	Syringic acid	p-Hydroxybenzoic acid	P-coumaric acid	Caffeic acid
Coconut water	4.15 ± 0.06^{A}	0.30 ± 0.16^{A}	0.12 ± 0.03^{B}	3.45 ± 0.07^{A}	0.50 ± 0.12^{A}
Fermentation broth	3.57 ± 0.17^{B}	0.30 ± 0.33^{A}	0.21 ± 0.02^{A}	2.88 ± 0.11^{B}	0.33 ± 0.03^{B}

In conclusion, the fermentation of coconut water by lactic acid bacteria increased total phenolic content, with a notable rise in p-hydroxybenzoic acid among the five monophenols analyzed, a reduction in epicatechin, caffeic acid, and p-coumaric acid, and no significant alteration in syringic acid.

Effect of *Lactobacillus* fermentation on volatile flavor substances of coconut water

In the present work, the influence of lactic acid bacteria fermentation on the volatile flavor substances of coconut water was further studied. The volatile organic compound (VOC) composition of each sample is shown in Fig. 4A and 4B. After fermentation, there was a significant increase in the number of volatile organic compound (VOC) species, which increased by 27 species. And the number of alcohols, esters and ketones was also enhanced. In addition, there was a significant increase in the number of organic acid species in the fermented samples compared to the unfermented coconut water. Long-chain hydrocarbons and cycloalkanes underwent cracking, oxidation and other reactions to produce other flavor substances due to the fermentation of lactic acid bacteria, and the content of alkanes decreased (Maghrebi et al. 2021). These changes had an important effect on the flavor of coconut water after fermentation.

During fermentation, changes in acids directly reflected the interaction between the metabolic activity of *Lactobacillus* and the raw material. Their dynamic balance determined the flavor, functionality, and stability of the product. Medium and long-chain fatty acids in coconut water underwent decomposition due to β-oxidation. The greatest increase in palmitoleic acid content among the organic acids was not detected in coconut water while it was produced in large quantities during the post-ripening stage (Fig. 4C, Table 3). Palmitoleic acid was capable of imparting specific flavors (e.g.

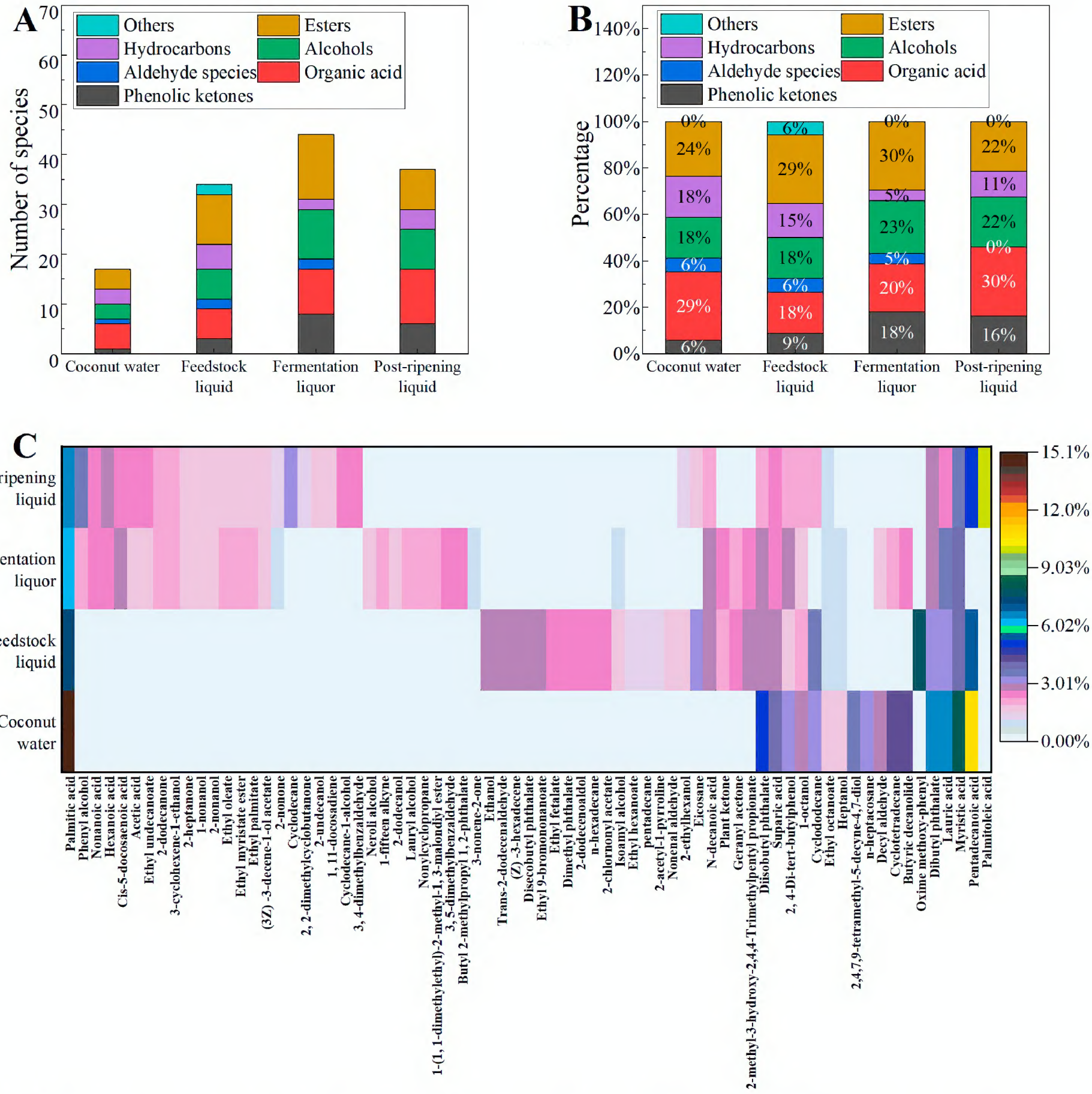

Figure 5. Changes of volatile flavor substances. **A.** Changes in the number of volatile flavorant species in coconut water; **B.** Percentage change of volatile flavorant species in coconut water; **C.** Organic heat map.

Table 3. Effect of fermentation on the content of volatile components.

Types	Organic name	Coconut water	Sterilization liquid	Fermentation liquid	Post-ripening liquid
	Palmitic acid	15.02%	7.35%	6.04%	6.47%
	Acetic acid	ND	ND	1.71%	2.27%
	Nonanoic acid	ND	ND	2.49%	2.56%
	Suparic acid	3.93%	2.83%	2.38%	2.43%
	Hexanoic acid	ND	ND	2.30%	2.93%
acids	Lauric acid	6.47%	3.26%	3.70%	2.28%
	N-decanoic acid	ND	2.69%	2.71%	2.03%
	Palmitoleic acid	ND	ND	ND	9.99%
	Myristic acid	8.17%	3.90%	3.93%	3.54%
	Pentadecanoic acid	10.82%	5.40%	ND	5.13%
	Cis-5-docosaenoic acid	ND	ND	2.92%	2.43%
	Phenyl alcohol	ND	ND	2.11%	3.58%
	Ethanol	ND	2.94%	ND	ND
	2-ethylhexanol	ND	1.72%	ND	1.48%
	Neroli alcohol	ND	ND	1.85%	ND
	Heptanol	1.70%	1.09%	1.04%	ND
	1-octanol	2.86%	2.07%	1.61%	1.99%
	Lauryl alcohol	ND	ND	2.14%	ND
Alcohols	Isoamyl alcohol	ND	1.65%	1.12%	ND
	2,4,7,9-tetramethyl-5-decyne-4,7-diol	3.41%	ND	ND	ND
	1-nonanol	ND	ND	1.65%	1.72%
	2-nonanol	ND	ND	1.54%	1.77%
	Cyclodecane-1-alcohol	ND	ND	ND	2.29%
	2-undecanol	ND	ND	ND	1.70%
	2-dodecenoaldol	ND	2.53%	ND	ND
	2-dodecanol	ND	ND	1.69%	ND
	3-cyclohexene-1-ethanol	ND	ND	2.06%	2.15%
	Diisobutyl phthalate	4.98%	2.69%	2.75%	2.22%
	Dibutyl phthalate	6.56%	3.27%	2.96%	2.95%
	Ethyl octanoate	1.72%	1.04%	0.91%	1.05%
	Ethyl fetalate	ND	2.50%	ND	ND
	Ethyl oleate	ND	ND	2.11%	1.87%
	Ethyl hexanoate	ND	1.18%	ND	ND
	Ethyl myristate ester	ND	ND	1.91%	1.77%
	Dimethyl phthalate	ND	2.54%	ND	ND
Esters	Ethyl undecanoate	ND	ND	1.65%	2.45%
	Ethyl palmitate	ND	ND	1.89%	1.80%
	Butyric decanolide	4.16%	ND	2.33%	ND
	2-chlornonyl acetate	ND	2.27%	ND	ND
	Butyl 2-methylpropyl 1, 2-phthalate	ND	ND	2.52%	ND
	Ethyl 9-bromononanoate	ND	2.66%	ND	ND
	methyl-3-hydroxy-2,4,4-Trimethylpentyl propionate	ND	2.84%	2.35%	ND
	(1, 1-dimethylethyl)-2-methyl-1, 3-malondiyl ester	ND	ND	2.13%	ND
	(3Z) -3-decene-1-ol acetate	ND	ND	1.82%	1.87%
	Disecobutyl phthalate	ND	2.77%	ND	ND
	Decyl aldehyde	2.95%	ND	1.71%	ND
	Nonenal aldehyde	ND	1.76%	ND	ND
aldehyde	3, 5-dimethylbenz aldehyde	ND	ND	2.54%	ND
	3, 4-dimethylbenz aldehyde	ND	ND	ND	2.39%
	Trans-2-dodecen aldehyde	ND	2.72%	ND	ND
	Eicosane	ND	3.19%	ND	1.79%
	Cyclodecane	ND	ND	ND	3.25%
	Cyclododecane	3.26%	3.44%	ND	2.18%
	Cyclotetradecane	4.32%	ND	2.17%	ND
	n-hexadecane	ND	2.41%	ND	ND
alkanes	pentadecane	ND	1.41%	ND	ND
	n-heptacosane	3.01%	ND	ND	ND
	1-fifteen alkyne	ND	ND	1.91%	ND
	1, 11-docosadiene	ND	ND	ND	1.70%
	(Z) -3-hexadecene	ND	2.78%	ND	ND
	Nonylcyclopropane	ND	ND	2.15%	ND

Types	Organic name	Coconut water	Sterilization liquid	Fermentation liquid	Post-ripening liquid
Heterocycles	2-acetyl-1-pyrroline	ND	1.44%	ND	ND
	Oxime methoxy-phenyl	ND	7.54%	ND	ND
Ketones	2-heptanone	ND	ND	1.64%	1.64%
	Plant ketone	ND	2.16%	2.30%	ND
	2-nonone	ND	ND	1.08%	1.32%
	2, 2-dimethylcyclobutanone	ND	ND	ND	1.31%
	Geranyl acetone	ND	2.61%	1.90%	ND
	2-dodecanone	ND	ND	1.92%	2.24%
	3-nonene-2-one	ND	ND	0.95%	ND
Phenols	2, 4-Di-tert-butylphenol	3.30%	1.75%	2.68%	2.22%

Notes: Data are presented as mean. ND: Not Detected.

creaminess) to food products and its formation might be related to the activation of Δ9-desaturase produced by *Lactobacillus* (Correa et al. 2021). Acetic acid production was not prominent, which was similar to the low content of acetic acid in *Lactobacillus* fermented coconut water reported by Zhang et al. (2018b). This might be related to the metabolic differences in *Lactobacillus* found in the study of Mousavi et al. (2011) and the properties of coconut water itself. Acetic acid together with short-chain acids such as hexanoic acid and octanoic acid could impart sour flavor to fermentation products and also participated in esterification to produce fruity lipids (Zhang et al. 2021; Huang et al. 2023). Cis-5-dodecenoic acid had potential functional activities in inflammation and immunity (Henry et al. 2002), and the increased content of this substance in fermented coconut juice suggested that the product had potential applications in this area.

Alcohols had an important influence on the flavor of foods. Changes in ethanol during fermentation might be related to the metabolism of saccharides, and the consumption of ethanol during fermentation and after-ripening reduced the production of pungent odors while providing precursors for the production of acids and esters. Phenylethanol was capable of imparting a rose aroma to food products, whereas heptanol, 1-octanol and 1-nonanol produced a grassy aroma that is detrimental to the flavor of fermented fruit juices (Fischer et al. 2021; Liu et al. 2023b). Upon fermentation, the increase in the former and the decrease in the latter resulted in a significant enhancement of the aroma quality. Lauryl alcohol was produced during fermentation, primarily to retain aroma. Consequently, it was consumed post-fermentation due to oxidation. Isoamyl alcohol was usually produced in connection with protein breakdown and produced undesirable flavors at higher concentrations. Its breakdown during fermentation and after-ripening contributed to the improvement of flavor.

Esters were usually associated with fruity aromas. Ethyl caprylate was an excellent flavoring substance associated with a fruity aroma (Liu et al. 2023b) and it was better preserved during fermentation. Ethyl oleate was able to contribute a more three-dimensional fruity aroma, while ethyl palmitate had a positive effect on aroma roundness, and their production greatly improved the flavor quality of the coconut water fermentation product, with a small amount of decomposition after post-ripening was possibly due to enzymatic action or oxidative breakdown (Liu et al. 2023b). Long-chain esters were associated with flavor persistence, and ethyl undecanoate increased both during fermentation and after post-ripening, resulting in a more persistent product flavor. However, fermentation by *Lactobacillus* caused the decomposition of anemone butyrate, which had a negative effect on the characteristic aroma of coconut, and inhibition of the reaction in question needed to be considered to avoid flavor loss. Microorganisms produced 3,5-dimethylbenzaldehyde in the matrix during fermentation, and this substance subsequently underwent the isomerization reaction 3,4-dimethylbenzaldehyde during post-ripening, both of which could produce flavors similar to almond or caramel (Wan et al. 2024). In contrast, the cheese aroma imparted by 2-heptanone might be generated due to the decarboxylation reaction of β-keto acids, again favored the fruity flavor of the product (Liu et al. 2023a). In addition, fermentation resulted in the reduction of heterocyclic substances while phenols were retained.

In conclusion, the co-fermentation of *L. paracasei* M1.5 and *L. casei* U2.1 had a positive effect on the flavor of coconut water while increasing the variety and content of beneficial components in coconut water.

Conclusion

In this study, *L. paracasei* M1.5 and *L. casei* U2.1 with good basal properties were screened for the co-bacterial fermentation of mature coconut water. The results indicated that fermentation by *Lactobacillus* significantly enhanced the total, free, and insoluble glycosidic phenolic content of coconut water. Furthermore, the fermentation process increased the diversity of volatile flavor components in coconut water by 27 species. The increase in alcohol, ester, and ketone levels further improved its organoleptic quality. For example, the accumulation of key flavor substances such as phenylethanol (rose aroma) and ethyl caprylate (fruity aroma), and the reduction of grassy flavor substances (e.g., 1-octanol) resulted in improved flavor. In addition, the increase in components with potential anti-inflammatory and immunomodulatory functions after fermentation, such as palmitoleic acid and cis-5-dodecenoic acid, conferred functional value to the product.

Therefore, lactic acid bacteria fermentation represents an effective approach for enhancing the flavor quality and nutritional value of coconut water.

Author contributions

Hao-Ran Zhang: experiments conduction, data processing and writing. Yu-Huan Wang: experiments conduction. Zi-Yi Peng: experiments conduction. Yun-Peng Hao:project administration, funding acquisition, writing and editing. Xiao-Peng Wang: supervision. All authors read and approved the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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